TORREYA

Vol. 41 March-April, 1941 No. 2

Floral Abnormalities in Linaria vulgaris

With Notes on a Method by Which New Genera May Arise

W. H. Camp and Charles Gilly

It is not unusual for zygomorphic (irregular) flowers to exhibit some form of abnormality by becoming partially or even completely regular. One of the more commonly observed types is that wherein flowers normally with one corolla spur produce five-spurred forms. This phenomenon was observed by the early botanists but seems to have been first given a name by Linnaeus.[1] He called it *Peloria,* meaning a prodigy or monster, a term derived from the Greek and applied to the abnormal forms of various flowers, particularly those of Butter-and-Eggs, *Linaria vulgaris* Hill,[2] with five spurs and five stamens. Masters[3] in his extended

[1] Linnaeus C. De Peloria. Pp. [vii] 18 [iv]. 1 plate. Upsala. 1744. Except for the various dedications and closing poetry, this is a dissertation written by Linnaeus and "defended" by one Daniel Rudberg before the faculty at Upsala. We were fortunate to have in the Library of the New York Botanical Garden a rare original copy of this thesis, and wherein the plate differs markedly from that of the more generally quoted and certainly better illustrated Amoenitates Academicae, at least that of the 1787 [3rd] edition which is before us. The texts of the two are essentially the same, thus explaining the difficulty one has in reconciling the plate of the Third Edition with its legend. It is also of interest to note that, here, peloria was considered a genus, although it was clearly recognized as consisting of abnormal states of various genera. Considering that this was written only nine years prior to the publication of the Species Plantarum, we can realize the state of flux in which the nomenclatural concepts of Linnaeus were during this period, for by 1753 he dropped peloria as a genus.

[2] *Antirrhinum Linaria* of Linnaeus' Species Plantarum, 1753.

[3] Masters, Maxwell T. Vegetable Teratology. London, 1869.

Torreya for January-February (Vol. *41*: 1-32) was issued February 7, 1941.
Torreya for March-April (Vol. *41*: 33-72) was issued April 21, 1941.

treatment of vegetable abnormalities has given us a rather full account of peloria (pp. 219–239) and distinguishes several types.

A plant of *Linaria* preserved in spirits and exhibiting various forms of peloria was recently brought to us for examination by Mr. Estil Kermit Handley (Figure 1). It was collected in a vacant lot on the west side of Garden Avenue between East Fifth Street and Sandford Boulevard, Mount Vernon, New York, in July, 1940. Mr. Handley kindly gave us permission to make a more detailed study of his specimen. At the same time we examined the specimens of the species on deposit in the herbarium of the New York Botanical Garden and found additional types of abnormalities, the more important of which are discussed in this paper.

In the normal flower of *Linaria vulgaris,* five nearly regular sepals are present. The five corolla segments are fused, their outer ends being represented by five lobes, two of which form the upper lip and the remaining three the lower. The spur is on the middle of the three segments forming the lower lip. The four functional stamens are didynamous and partly fused to the base of the corolla, the fifth being represented either by a minute vestigial structure or is absent, no evidence of it having been found in certain instances, even under the higher powers of the microscope.[4] It is the stamen whose position would lie between the two lobes of the upper lip of the corolla which has been suppressed. The ovary is two celled, the septum being nearly in a plane with the split between the lips of the corolla. (For details see Figures 10a–c, 11.)

It will scarcely be necessary to take up in any great detail the various forms encountered in this study. The Handley specimen from Mount Vernon, New York, indicates that there is, necessarily, no sudden change from the normal to the peloric state. Instead, it is quite likely that there may be a gradual shifting of physiological gradients both within the developing inflorescence

[4] In this study we have had no opportunity to make any detailed observations either of the vascular supply or modulus of variation of stamens within any great number of what otherwise—and from their external appearance—would be considered normal flowers. However, in a series of plants from various localities we have noted a tendency for one or both of the shorter pair of stamens to be either longer or shorter than usual; also, that the pattern of the vascular supply of those flowers which have no remnant of a fifth stamen is somewhat different from those which have it, at least in that portion of the corolla adjacent to the abortive stamen.

and individual flower so that there are successive stages in the development of complete peloria.[5] For example: one flower (Figures 2a-c) was normal except for small spurs on the lateral corolla segments of the lower lip, the fifth stamen being represented by a minute tab of sterile tissue attached to the base of the corolla. Another (Figures 3a-c) was essentially the same, except that the fifth stamen, although smaller than any of the others, bore two pollen sacs. In complete peloria (Figures 4a–e) five spurs and five equally developed stamens are present.

As has been mentioned in the brief description of the normal flower, the single spur is found on the middle one of the three segments of the lower lip. It may also be noted in the normal flower (Figure 10c) that it is the lower lip which is refolded, forming the thickened labium characteristic of this portion of the corolla. Partial peloria (as Figures 9a–b) may have a somewhat narrowly tubular corolla with the lips reduced. Where peloria is fully developed, all five segments of the corolla bear spurs; also the apex of the corolla has the double fold (*i.e.,* of a type characteristic of only the lower lip in the normal form) present and involving all five segments (see Figures 4d–e). Apparently those factors which are involved in the production of the middle segment of the lower lip of the normal flower, with its spur and refolded labium, have become active in all five segments of the corolla. It is also interesting to note that this example of complete peloria had five equally developed stamens and a tri-carpellate ovary and thus, by a strict interpretation of the generally accepted family characters, could not remain in the Scrophulariaceae with the other flowers of the same inflorescence.

It is outside the province of this paper to more than speculate on the origin and evolution of various flower forms, but abnormal material such as this will undoubtedly present various clues useful in the ultimate untangling of many of our phyletic concepts. In *Linaria,* it is obvious that the fifth stamen, instead of being eliminated by the advent of zygomorphy has only been suppressed, for it takes but little disturbance of the normal ontogenetic pattern to reproduce the structure in a completely normal form. This, then,

[5] For an account of the difficulties met in an attempt to fix the hereditary condition of peloria in *Linaria,* see De Vries, The Mutation Theory, English Ed. Vol. 2: 201-220. 1910.

brings up the following problem: Was the primitive form from which the modern *Linaria* evolved one with five spurs, or did the normally single spur evolve after the onset of zygomorphy? The present writers are inclined toward the latter viewpoint.[6]

Other flowers on the Handley specimen (as Figure 5 with its bifurcate spur and Figures 6a–8c with supernumerary anthers and incomplete peloria) are of interest if only to indicate the potentiality for plasticity of ontogenetic variation within the developing organs of a single individual. It will be noted (particularly in Figures 6a–8c) that there seems to be a spatial relationship between the production of functional supernumerary anthers and the development of supernumerary spurs. The external views and floral diagrams of these flowers will be self-explanatory.

During our examination of herbarium material we came upon a series of specimens collected by R. Hitchcock near Van Cortlandt Park, New York City, in June, 1909. Although no two flowers of this collection were exactly alike, it was unusual in that the various ones examined had the same general types of abnormalities: they were smaller than is normal for *Linaria vulgaris*; the spur was lacking or but poorly developed; the corolla, although bilabiate, was irregularly erose; and, still more remarkable, in addition to the four normal stamens, additional rudimentary stamens or anther pouches were found (see Figures 12a-14e). In every case these were attached to or partly imbedded in the tissues of what ordinarily would have been the lower of the two corolla lobes (*i.e.,* the one composed of three corolla segments, the middle one of which ordinarily would have borne the spur).

There is but little point in discussing this phenomenon without having worked on the living material, but studies some years ago by the senior author on other species (principally *Cannabis sativa,* the results of which are not yet completely published) indicated a close relationship between a disturbance of the normal sequence of metabolic rates within developing flower primordia and the production of such monstrosities. It is to be here noted as

[6] The reader will undoubtedly think of analogous problems, as for example in the Ranunculaceae where *Delphinium* has one of the perianth segments produced into a spur, or in *Aquilegia* where spurs are found on five perianth segments (although admittedly in a different cycle from that of *Delphinium*). The genus *Aconitum* is also subject to peloric forms.

a corollary that a definite morphological gradient exists in the normal flower of *Linaria:* the upper (adaxial) stamen is suppressed, the next two stamens are intermediate in length, and the lower (abaxial) stamens are longest; the lower lip of the corolla has the greatest marginal hypertrophy (as shown by its refolded labium) and it is also from the middle of its three segments that the spur is produced. Obviously it is this abaxial segment of the developing flower primordium which is normally most active, both physiologically and ontogenetically. Also it is in (or on structures produced by) this region where we find the greatest number of abnormalities which, in the final analysis, are only visible proofs of unusual physiological activities resulting in abnormal morphological structures.

Of further interest was a series of specimens collected by John McCallum, near Morris Park, Long Island, in 1912. It involved a series of plants exhibiting several types of peloria, including both spurless and multiple-spurred forms. Of these we will consider only one flower (Figures 15a–c). Here the spur was absent; also there was good evidence that the middle segment of the lower lip of the corolla had been lost, each lip, therefore, consisting of two corolla segments. Substantiating the view that one entire segment of the flower was lacking was the fact that the calyx had but four segments, with no evidence of fusion between lobes; also the flower bore but three stamens. When one compares the diagram of this flower (Figure 15c) with that of a normal flower (10b), it is obvious that, in addition to one sepal and one corolla segment, one of the abaxial stamens had been lost. Thus, there was achieved an essentially tetramerous flower modified only by its inherent zygomorphy, and this evident by a residual bilabiate condition.

Going outside the Torrey Club Area for material, we have a series of plants collected by William Scott at York Mills, near Toronto, Canada, September 18, 1911. Judged only by the flowers, this material could by no stretch of definition be placed in the genus *Linaria,* although there was no mistaking the plant's habit. The flowers were almost completely regular, with four sepals, four corolla segments, two anthers and a two-carpelled ovary (Figures 16a–c). The collector's notes state that it "grows in great profusion in at least four localities within about five miles of Toronto. . . . . I think it does not set seeds but propagates itself simply from

root stocks. There can be no doubt that it is established here for this is the second year that I have seen it and I could collect a waggon load of it if necessary."

It is quite likely that the material was sterile, as noted by the collector, and that it depended on vegetative reproduction for survival. Knowing nothing of the cytology of this particular group of plants, one can do no more than speculate on its origin. However, it is safe to assume that the variety of characters in which it differed from the normal form was not due to a single-gene mutation, but involved a series of more drastic changes—none of which was lethal to a plant able to propagate itself vegetatively, as did this plant, forming a series of clones.

Plate I

FIGURES 1–9b. LINARIA VULGARIS HILL

Figures 1–8c. Collected by Estil K. Handley, Mount Vernon, New York, July, 1940.

1. The single plant showing the various flower types.

2a. External view of a flower bearing two small lateral spurs; 2b, its floral diagram indicating the presence of four functional stamens and one vestigial stamen, as shown in 2c, the details of the reproductive organs.

3a-b. External view and floral diagram of a flower similar to the above, but with the fifth stamen somewhat more developed and bearing two pollen sacs. The details of the reproductive organs of this flower are shown (in 3c) enlarged.

4a–e. The completely peloric flower. 4a, external view; 4b, its floral diagram, the five spurs, five stamens and tricarpelled ovary may be noted; 4c, median section; 4d, external view of the apex of the corolla; 4e, median section showing its refolded lip.

5. Flower with bifurcate spur.

6a–b. Flower with two well developed spurs and one small spur. A supernumerary stamen was present between the larger spurs but the "fifth" (adaxial) stamen was represented only by a tab of sterile tissue, much as in Figure 2c.

7a–b. A flower essentially similar to the preceding, but differing in having the floral pattern reversed; also the "fifth" stamen bore a two-celled anther, much as in Figure 3c.

8a–c. Face and lateral views, and diagram of a flower with three spurs and six stamens; the "fifth" stamen was fully developed and the supernumerary stamen was attached to the receptacle opposite the median spur. Here the flower was assuming a balanced symmetry.

9a–b. A specimen from the Torrey Herbarium (locality and collector unknown but probably by John Torrey in the vicinity of New York City). Here, two spurs had been developed; also, the apex of the corolla was approaching the form of that assumed in complete peloria.

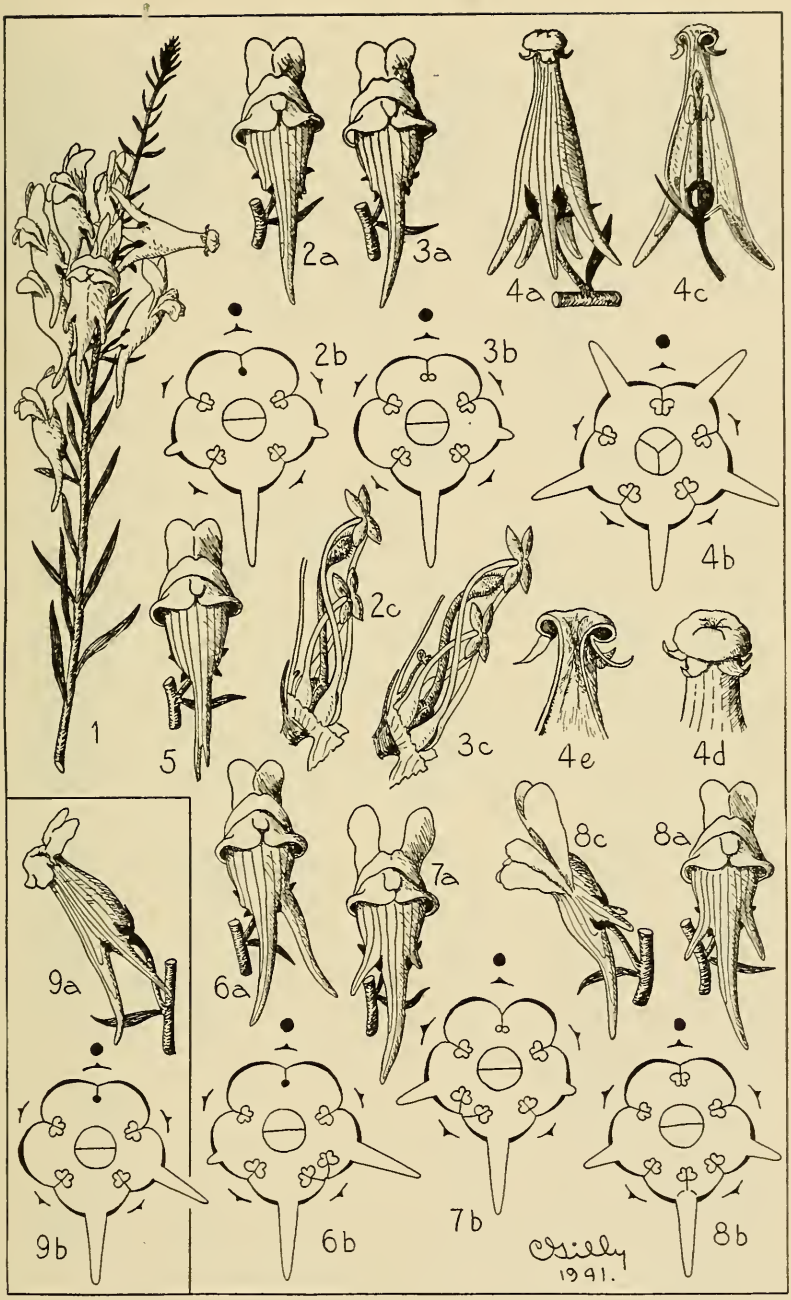
1
2a
3a
4a
4c
2b
3b
4b
5
2c
3c
4e
4d
9a
6a
7a
8c
8a
9b
6b
7b
8b
Reilly
1941.

Plate 1

From what we now know about the cytology of such organisms, it is reasonable to assume that, like so many similar cases, autopolyploidy[7] could easily bring about a population of completely

[7] *Autopolyploidy*—the doubling of the number of chromosomes of a form without prior hybridization; as contrasted with *allopolyploidy*—the doubling of the number of chromosomes of an individual the product of hybridization. In either case the resulting forms generally produce sufficient seed to maintain themselves under favorable environmental conditions.

Plate II

FIGURES 10a–16c. LINARIA VULGARIS HILL

Figures 10a–c, and 11. Normal flowers collected in Bronx Park, New York City, summer of 1940, by C. Gilly.

10a–b. External view and floral diagram of a flower with four stamens but with no evidence of the "fifth"; 10c, median section showing the relations of the internal parts to the spur and particularly the refolded nature of the labium on the lower lip of the corolla; 11, diagram of an otherwise normally appearing flower bearing two anther sacs on the "fifth" stamen much as in Figure 3c.

Figures 12a–14e. From a series of plants collected by R. Hitchcock, near Van Cortlandt Park, New York City, June, 1909.

12a–b. External views showing a rare condition in this collection, with five sepals and a small saccate enlargement in place of the spur; 12c, the corolla laid open showing the four normal stamens and minute supernumerary stamen structures on the lower lip; 12d, further enlargement of the apex of the lower lip of the corolla showing the supernumerary stamen-like structures near its margin.

13a–b. External views showing the more common condition with four sepals and no evidence of a spur; 13c, the corolla laid open showing the four normal stamens, several well developed stamen structures, and various sessile anther pouches.

14a–b. External views of a flower essentially similar to the preceding; 14c, its corolla laid open to show the position of the supernumerary anther and anther pouches near the margin of its lower lip; 14d–e, further enlargements of the lateral portions of the lower lip showing details of the supernumerary anther and several anther pouches.

Figures 15a–c. From a collection by John McCallum, Morris Park, Long Island, New York, in 1912.

15a–b. Two views of the same flower; 15c, its floral diagram.

Figures 16a–c. From a collection by Wm. Scott, York Mills, near Toronto, Canada, September 18, 1911.

16a–b. External views of a flower; 16c, its floral diagram showing four sepals, four corolla segments, two stamens and the bi-carpelled ovary.

FIGURES 17a–b. VERONICASTRUM VIRGINICUM (L.) FARWELL

From typical material deposited in the Herb. N. Y. Botanical Garden. 17a, external view; 17b, floral diagram.

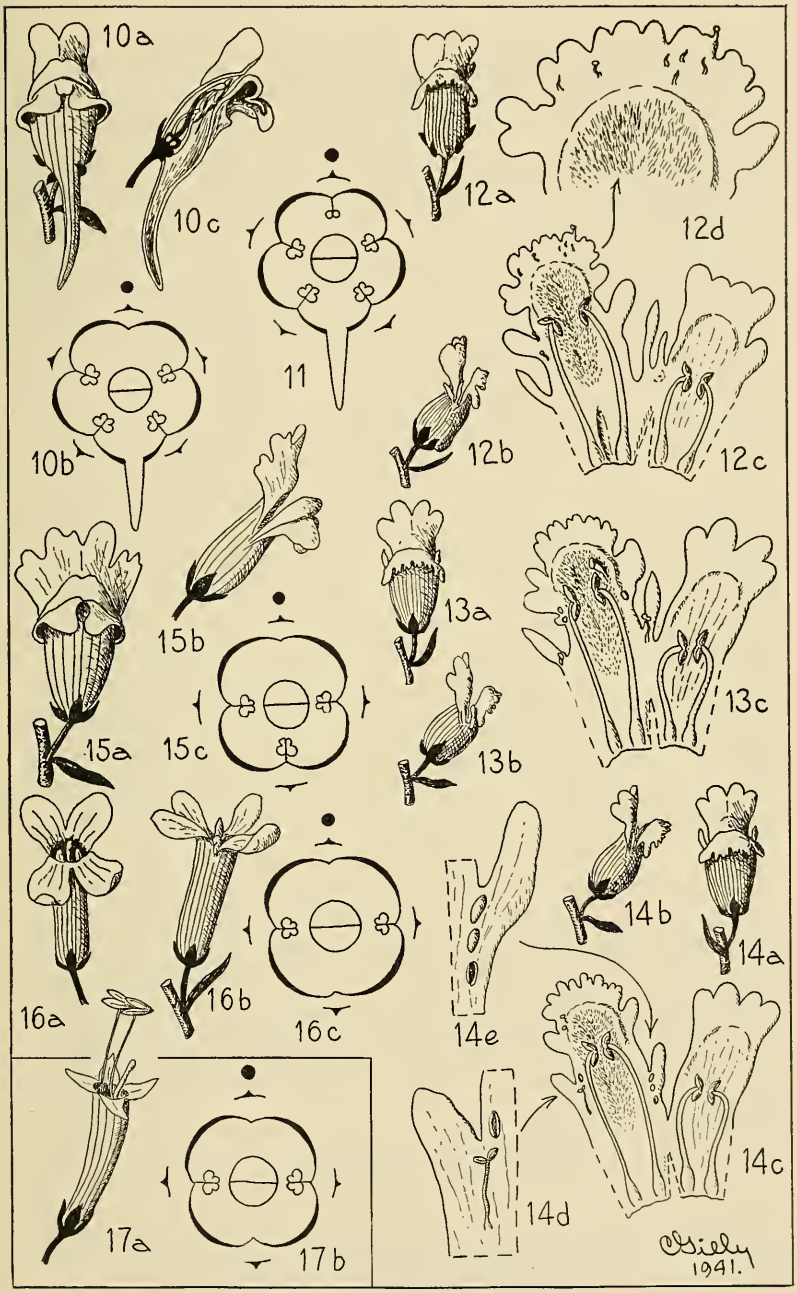
10a
10c
11
12a
12d
10b
12b
12c
15b
13a
13c
15a
15c
13b
16a
16b
16c
14e
14b
14a
14c
14d
17a
17b
1941.

PLATE 2

fertile plants propagating and spreading themselves by means of seed. And thus would arise a race of plants with a stable heredity—and in this instance a race so different from the ancestral *Linaria* that any taxonomist seeing it for the first time would place it in the Scrophulariaceae, but would be *completely justified in describing the group as a new genus.*

While on this topic of the possible origin of taxonomic units above those of species, one cannot help but point out the structural similarity of the flowers of this unusual form of *Linaria* (as shown by Figures 16a–c) and that of the common Culver's root, *Veronicastrum virginicum* (Figures 17a–b). Although members of the same family, it is not implied that these two plants are of immediately mutual derivation. It is suggested only that the reduced condition of the nearly regular flowers of *Veronicastrum* (occurring as it does in a family with so much zygomorphy) may have been derived in a manner somewhat similar to the reduced and nearly regular forms of *Linaria vulgaris* with, of course, the advent of fertility due, possibly, to polyploidy of one sort or another. The possibility that *Veronicastrum* may be an anomalous genus the result of convergent evolution and is placed in the Veroniceae solely on the basis of its flower structure—with but little regard for the whorled condition of its leaves—must not be excluded from any ultimate discussion of the phylogeny of the group. It is our opinion that *Veronicastrum* is not necessarily a primitive member of this tribe as Pennell[8] has suggested.

For some years the study of "abnormal" flowers has been frowned upon by the systematist, but it is our opinion that if these forms are examined more closely in the future they will shed considerable light on the mechanics of the origin of the larger taxonomic units, such as genera and even families. This will be true particularly if these abnormalities are looked upon not merely as vegetable curiosities, but are studied both from the anatomical and cytological standpoint.

The New York Botanical Garden,
New York, N. Y.

[8] Pennell, F. W., "Veronica" in North and South America. Rhodora 23: 1-41. 1921. The Scrophulariaceae of eastern temperate North America. Phil. Acad. Nat. Sci. Monog. No. 1. 1935.